

## Observations on the Nature of Parasitism

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BIOLOGISTS generally agree that parasites arose from free-living forms. The proof for this is quite conclusive, as pointed out by Wenrich (1935). Evidence is sparse, however, in support of the contention held by many that endoparasitic forms arose from ectoparasitic ones.

The specificity existing between parasites and their hosts is one of the more basic problems confronting parasitologists today. This phenomenon is of interest from the viewpoints of the biochemist, the taxonomist, and the student of evolution, as well as to the parasitologist.

Wenrich (*op. cit.*) postulated that host specificity among parasites arose along two main lines. One of these was followed by parasites which became adapted to a large variety of hosts. Among the protozoans perhaps the trypanosomes are the outstanding examples. They successfully parasitize hundreds of vertebrate species from all major classes. Another wide-ranging protozoan genus is *Eimeria*, various members of which are parasites of annelids, arthropods, and vertebrates. Faust, Beaver, and Jung (1962) name the heterophyid digenetic trematodes as examples of parasites capable of infecting a wide range of hosts; these flukes can become established in all birds and mammals which infest infected raw or poorly cooked fish.

The second line of evolution was followed by parasites which have become associated with one or, at most, a few host species. The trend toward close host-specificity is well exemplified by the monogenetic trematodes.

Hargis (1957) performed a revealing analysis of monogeneid host-parasite relationships in a study conducted at the Oceanographic Institute of Florida State University. He recovered 3,338 monogenetic trematodes (representing 75 species) from 415 hosts specimens (representing 49 species). He found that 68 species (89 per cent) of the parasites were specific for a single species of host. The remaining eight species (11 per cent) parasitized more than one host; of these, seven occurred on two host species, while only one was associated with three different hosts.

Dr. Harold Manter (1962), in reviewing portions of Bychowsky's (1957) monograph on the Monogenea, summarized the host-parasite relationships for all monogeneans known at that time. Of the total of 958 species of Monogenea, 806 (84 per cent) were known only from a single genus of host, while 711 (74 per cent) were parasites of a single host species. Further, he found that only 18 species occurred on fishes belonging to more than one order.

So close is the specificity of monogenean parasites for their hosts that Mizelle et al. (1943) and Hargis (1957) reported that in cases hosts could be identified by determining the species of Monogenea parasitizing them. I have also found this to be true on several occasions.

In an unpublished study, I removed the gills from 300 host specimens of the mosquitofish, *Gambusia affinis affinis* (Baird and Girard). More than 1,000 gill trematodes were recovered; without exception, these parasites were identified as *Urocleidus seculus* Mizelle and Arcati, 1945, described from this fish species more than 20 years before.

As pointed out by Hargis (1957) accidental parasitism, i.e., the occurrence of a monogenean parasite on the "wrong" host, is exceedingly rare. Even among aquarium fishes which live in tanks shared by several species of both related and unrelated forms, the incidence of accidental parasitism by monogeneans is very low.

#### INTRASPECIFIC VARIATION AS A FUNCTION OF HOST-SPECIFICITY

Intraspecific morphological variation of parasites is apparently related to the specificity of a parasite for a certain host or hosts. Certain monogeneans which are capable of infesting different host species often seem to fare better on one host than on another. Price and Mizelle (1964) recovered and described a new gill trematode, *Dactylogyrus microlepidotus*, from the cyprinid fish *Orthodon microlepidotus* (Ayres). A few days afterward, what at first appeared to be an additional new *Dactylogyrus* was recovered from the gills of another minnow, *Lavinia e. exilicauda* Baird and Girard. Further comparative study disclosed that the two *Dactylogyrus* "species" were in actuality only size variants of a single new species. The apparent dissimilarities in the two variants were due to pronounced discrepancies in relative sizes of the worms. Trematodes from *Lavinia*, e.g., averaged 109 per cent greater overall length.

In the same study several goldfishes, *Carassius auratus* (L.), were examined for gill trematodes. Among those recovered were three Old World species, viz., *Dactylogyrus anchoratus* (Dujardin), *D. vastator* Nybelin, and *D. wegneri* Kulwiec. No significant qualitative variations of a morphological nature were observed, but in comparison with descriptions of these parasites from Europe and Japan, the American forms were much smaller.

In light of these and similar findings, it would seem that size alone is a poor criterion upon which to establish new species.

#### THE BASIC NATURE OF HOST-PARASITE RELATIONSHIPS

The mechanisms of host-specificity are not fully understood as yet, but the phenomenon is being studied by many workers. That this attraction of parasite to host is chemical in nature, however, has been quite well established.

O'Rourke (1961) has shown that each species of fish apparently secretes a specific mucus from its body and gills. Chromatographic studies demonstrated that piscine species can be differentiated by analysis of constituent serum proteins present. O'Rourke (*op. cit.*) went on to show that many of the serum proteins of a given fish species were also present in the mucus. Since the serum protein complement of a given organism has invariably been shown to be species-specific, it follows that the mucus would likewise be species-specific, as most of the serum antigens were contained in the secreted gill and body mucus. As it appears quite certain that parasites are attracted to their hosts by chemotactic mechanisms, the parasites of fishes might conceivably contact their hosts by "specific attraction" of the parasite by the species-specific serum antigens of the fish host.

#### REQUIREMENTS FOR SUCCESSFUL PARASITISM

Chandler and Read (1962) have pointed out that in order for a parasite to become successfully associated with a host, three requirements must be met: (1) suitable conditions for access to the host must be available, involving a dependable means of transmission from one host to another; (2) the ability to successfully establish itself upon reaching the host, and (3) satisfactory conditions for growth and reproduction after it becomes established. It is the interplay of these factors that determines the degree of a parasite's success in becoming established within or on a given host.

## HOW THE MONOGENEA HAVE MET THESE REQUIREMENTS

Members of the strigeid (digenetic) trematode genus *Alaria* require four successive hosts during their life cycles. In addition to the usual miracidial, sporocystic, and cercarial forms utilized by most Digenea, *Alaria* species require a fourth, the mesocercarium; *Alaria* and its larval stages must in turn live in a snail, a tadpole, a mouse, and a mink (Chandler and Read, 1962). It would obviously be to the advantage of an ambitious parasite to eliminate as many of these intermediate stages as possible, for each transfer is fraught with hazards.

The Monogenea, as reflected in the name ascribed to them, have direct life cycles, i.e., they do not require intermediate hosts in the courses of their life histories. During their early existence monogeneid larvae are free-swimming, being provided with cilia for this purpose. This free-swimming organism stands a much better chance of achieving success in its quest for a host without spending variable periods of time in intermediate hosts while en-route to the definitive host. As these worms are androgynous, it seems plausible that only a few viable larvae need contact a host in order to give rise to an infestation.

Perhaps the biggest factor involved in overcoming the second and third conditions is compatibility of the parasite with the host from an immunological viewpoint. Hosts possessing adequate immunological defenses are refractory to many potential parasites; some are apparently completely refractory to invasion by gill trematodes. If the invading parasite proves to be chemically compatible with the potential host, a major obstacle has been overcome, as far as the parasite is concerned.

Another necessity is a provision for attachment to the host's tissues. In his monograph, Bychowsky (1957) shows that larval stages of monogeneans are equipped with a number of haptorial hooks for purpose of attachment. These hooks are referred to as "larval hooklets" by both Bychowsky and by Yamaguti (1963). These structures persist in most species and seemingly become abortive in a few, but all are functional for attachment in the larval stages. The larva of *Dawestrema* (Price and Nowlin, 1967), for example, possesses a pair of anchors and seven pairs of hooks at a post-embryonic stage in which the volume of the parasite is less than that of the egg from which it came.



Special copulatory devices for insurance of fertilization are necessary provisions for organisms that must sometimes conduct copulation at relatively enormous distances and often under conditions of turbulence and pronounced water flow. Such copulatory devices are present in great diversity among the Monogenea.

An example is *Telegamatrix pellone* (Ramalingam). These gill flukes are able to copulate at relatively great distances by means of a copulatory tube equipped with two-way ducts. Such a device is immensely efficient in achieving fertilization in habitats that constitute many hazards to inhabitants which would otherwise find it necessary to change locations frequently.

*Dawestrema*, referred to above, is provided with a cirrus (male intromittent organ) arranged in a large coil of six turns. When fully extended, the cirrus is approximately one-half as long as the parasite's body.

Members of the genus *Diplozoon* have approached the problem of insuring fertilization in a quite different manner (Bychowsky, 1957). A post-embryonic stage termed a "diporpa" is reached. Two of these forms become fused together after attaching to each other by median genital orifices. The male genitalia of each undergoes anatomical fusion in the female orifices of its partner. The result is a state of permanent copula; such an arrangement obviously goes far in assuring continuation of the species.

Another interesting mechanism is the specialized method of embryology of *Gyrodactylus* species (Bychowsky, 1957). Examination of adult gyrodactylids reveals in most cases a well-formed embryo in the uterus. Close examination will often disclose the presence of a smaller but discernible embryo within the uterus of the first embryo. Some workers note that they have observed a third embryo within the second and Hyman (1951) states that a fourth embryo can sometimes be seen. When the larger of the embryos has matured sufficiently it passes to the exterior, the remaining embryos still enclosed within it. The larvae attach directly to the host upon emergence from the birth pore.

#### CONCLUDING NOTE

The study of parasite-host relationships in future years will doubtless yield many significant findings for biologists. The biochemical approach to this field of study has already furnished en-

lightenment on many aspects of this association and will certainly continue to furnish more. The study of morphology and the taxonomy based upon morphology, continue to play significant roles in new findings. The search for truth is always made more efficient by a coordinated effort.

#### SUMMARY

Lines of evolution occurring among parasite groups are briefly commented upon. Some aspects of intraspecific variation among Monogenea are touched upon. After this the necessary steps for successful parasitism are recounted. Finally, examples are given illustrating how monogenetic trematodes have become an especially successful group of parasites.

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